A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 97: 257–277 (2025)
DOI: 10.3897/neobiota.97.126607

Research Article

Non-native species drive the global loss of freshwater fish beta-diversity

Lorraine L. Cavalcante[1], Thiago V. T. Occhi[1], Julian D. Olden[2], Andre A. Padial[1,3]

1 *Postgraduate Program in Ecology and Conservation, Analysis and Synthesis in Biodi-versity Laboratory, Department of Botany, Biological Sciences Sector, Federal Uni-versity of Paraná, Curitiba, Paraná, Brazil*
2 *School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA*
3 *Postgraduate Program in Ecology of Continental Aquatic Environments, Research Center for Limnology, Ichthyology, and Aquaculture, State University of Maringá, Maringá, Paraná, Brazil*

Corresponding author: Andre A. Padial (aapadial@gmail.com)

Abstract

Freshwater ecosystems are facing mounting challenges. The widespread introduction of non-native species, for example, has resulted in the loss of native species and the substantial reconfiguration of diversity patterns across regions. Documenting such impacts remains critical for informing national-level biosecurity policies. Here, we explore changes in biogeographic patterns in freshwater fish diversity in response to the spread of non-native species, teasing apart the geographic (watersheds) and taxonomic (species) drivers of patterns at the global scale. We leveraged global databases of fish species occurrence to estimate the unique contributions of local watersheds and species (native and non-native origin) to beta-diversity for biogeographic domains. Beta-diversity metrics of watersheds and species at a domain scale can be interpreted as their importance for the uniqueness in freshwater fish composition. We report significant changes in freshwater fish beta-diversity in response to non-native species, with the largest impacts in the Ethiopian, Nearctic and Palearctic domains, even though non-natives decreased the contribution of watersheds to beta-diversity in all domains, particularly in watersheds with known impacts. Watersheds identified as most important for promoting beta-diversity were not evenly distributed across domains, were influenced by geographical isolation and their unique compositions were composed of many endemic and threatened species. Highest values of species contributions to enhancing beta-diversity were mainly observed for native and threatened species, although mean values of species contributions were higher for non-threatened species. Species from the most important watersheds had wide ecological tolerances, were, in general, natives, endemics and/or with IUCN threat status. Our findings underscore the widespread consequences of non-native species for shaping biogeographic patterns of freshwater fishes in the Anthropocene.

Key words: Beta diversity, biodiversity conservation, biogeographic domain, biotic homogenisation, exotic species

OPEN ACCESS

Academic editor:
Jonathan M. Jeschke
Received: 30 April 2024
Accepted: 24 December 2024
Published: 24 February2025

Citation: Cavalcante LL, Occhi TVT, Olden JD, Padial AA (2025) Non-native species drive the global loss of freshwater fish beta-diversity. NeoBiota 97: 257–277. https://doi.org/10.3897/neobiota.97.126607

Copyright: This is an open access article distributed under the terms of the CC0 Public Domain Dedication.

Introduction

Limitations on dispersal ability have produced the interesting phenomenon that many, perhaps even most, species do not occupy all the areas of the world in which they could survive (Darwin 1859). This is perhaps no better demonstrated than in freshwater ecosystems, where high diversity and endemism stem largely from the fact that freshwaters are embedded within a terrestrial landscape that limits

dispersal within and amongst drainage basins (Olden et al. 2010). River basins or watersheds act as "islands" where fish evolution occurs somewhat independently (Tedesco et al. 2012; Su et al. 2019). As a consequence, a complex combination of factors shapes broad-scale diversity patterns of freshwater fish, including the palaeo-connectivity of watersheds, eco-evolutionary processes and environmental variability interacting at different scales (Leprieur et al. 2009; Dias et al. 2014; Carvajal-Quintero et al. 2019).

The regional connectivity of the world is stronger and more varied than ever before. In this sense, human-induced biological invasions have been growing in the last centuries and there is no indication that rates are decreasing to a saturation level (Seebens et al. 2017). It is now a consensus that biological invasions cause impacts not only at local scales, but are also responsible for a global reshuffling of biogeographic patterns (Leroy et al. 2023), leading to biotic homogenisation of ecological communities (McKinney and Lockwood 1999). The widespread introduction of non-native species has dramatically reconfigured patterns of diversity, often leading to the loss of native species (Pyšek et al. 2020; Su et al. 2021) and the dissolving of biological uniqueness across regions (McKinney and Lockwood 1999; Olden 2006). Such homogenising effects are ubiquitous across spatial scales and taxonomic groups, particularly for freshwater fishes (Olden et al. 2018; Padial et al. 2020). Human-mediated dispersal of non-native freshwater fishes occurs as a result of numerous pathways, including aquaculture practices, ornamental pet trade, release of bait for angling, biological control, stocking for fisheries, shipping ballast transport and interconnected waterways amongst others (Bernery et al. 2022). The features that explain successful establishment of non-native species (i.e. invasiveness) together with the characteristics of the receiving environment (i.e. invasibility) interact to produce the patterns of invasions (Skóra et al. 2015; Hui et al. 2016; Xu et al. 2024).

The impacts of non-native species introductions are truly global in scale (Seebens et al. 2017; Capinha et al. 2022) and the homogenisation of freshwater fish faunas in response to non-native species is increasingly recognised [e.g. Leprieur et al. (2008); Olden et al. (2008); Marr et al. (2013); Liu et al. (2017)]. The change is so dramatic that even well-accepted biostratigraphic boundaries for biological communities, known as biogeographic domains, are being re-arranged in the Anthropocene, creating new domains such as the 'Pan-Anthropocenian Global North and East Asia' (PAGNEA, *sensu* Leroy et al. 2023). For freshwater fish faunas, such dramatic modifications pose a significant concern (Olden et al. 2010; Cucherousset and Olden 2011), as preserving broad-scale beta-diversity is a priority in large-scale conservation planning (Socolar et al. 2016; Su et al. 2019). At the same time, changes in the fish community may cause impacts on the ecosystem services provided by them, such as the provisioning of food (i.e. fisheries and aquaculture), the regulation of pest controls (i.e. insects), the supporting of nutrient cycling and ecosystem engineering, as well as many cultural services associated with traditional culture and fishery (Pelicice et al. 2023).

The Emergency Recovery Plan required to "bend the curve" in freshwater biodiversity loss explicitly calls for a renewed focus on preventing the impacts of non-native species (Tickner et al. 2020). The recovery plan and its recommendations are aligned with several sustainable development goals and targets of the Kunming–Montreal Global Biodiversity Framework (2022) aiming to restore and recover biodiversity by 2050. Recovery planning must ensure the conservation of native fish biogeography in the light of past and likely future species invasions (Britton et al. 2023). In this sense, describing patterns in beta-diversity studies

is central to better providing information for conservation efforts (Socolar et al. 2016); and a meaningful scale for freshwater fish are watersheds within biogeographical domains [e.g. Tedesco et al. (2017); Leroy et al. (2019)]. For instance, changes in beta-diversity indices amongst watersheds may provide information for the impact of non-native fish species on the biogeographic patterns of continental aquatic environments. Additionally, beta-diversity patterns indicate those watersheds and species that are most important for promoting regional compositional differences and combatting growing trends towards a more homogenised world. For instance, the watersheds and species that mostly contribute to compositional uniqueness in the biogeographic domain would be those deserving conservation efforts to mitigate biotic homogenis ation (Xia et al. 2022).

Here, we sought to disentangle the roles of native and non-native species in shaping contemporary patterns of freshwater fish beta-diversity across biogeographic domains of the world. We identify and map watersheds that remain strongholds in enhancing fish beta-diversity and determine those species contributing the most to these patterns. By elucidating the pattern and drivers of changes in freshwater fish beta-diversity, we aim to provide information for national and international policies and conservation strategies that seek to preserve the uniqueness of the world's fish fauna in the light of ongoing species introductions.

Material and methods

Ichthyofauna global database and biogeographic domains

The compositional data by river watershed in the biogeographic domains were obtained from the ichthyofauna database published by Tedesco et al. (2017). The database contains species lists for > 3,000 watersheds covering more than 80% of the Earth's surface and includes nearly 15,000 fish species inhabiting permanently or occasionally freshwaters. The database was based on surveys of 1,436 published papers, books, grey literature and web-based sources (Tedesco et al. 2017). Watersheds were organised according to biogeographic domains that were proposed by Leroy et al. (2019) as meaningful regions for freshwater fish: Australian, Ethiopian, Madagascar, Nearctic, Neotropical, Palearctic and Sino-Oriental. Indeed, Muñoz-Mas et al. (2023) already demonstrated that this classification is suitable to understand global patterns of freshwater fish invasions. We updated the database by omitting extinct species according to the revision by Su et al. (2021) and by classifying non-native species as those originally foreign to the biogeographic domain, but introduced directly or indirectly by humans. Metadata and complete sheets of species occurrence per watershed are freely available for download at <https://doi.org/10.1038/sdata.2017.141> and classifications of biogeographic domains are available at <https://borisleroy.com/fish-biogeography/>. The Madagascar domain was not used, given the low number of watersheds, making beta-diversity analyses meaningless.

Watersheds were differentiated by exorheic (watersheds having an estuary with an outlet to the sea or ocean) and endorheic (watersheds not having an outlet to the sea or ocean). Species origin was confirmed according to the Global Invasive Species Database – GISD (Pagad et al. 2015) and the Invasive Species Compendium (CABI 2021). Once the database was updated, we used the "fishbase.valid.name" record as the official record of species by watershed. Updates to the current species name or its classification into subspecies were also made when necessary.

Beta-diversity indices

Beta-diversity (β) – a measure of the amount of change in species composition from one location to another (Whittaker 1972) – can be partitioned into unique variations contributed by individual sites and species within the dissimilarity matrix (Legendre and De Cáceres 2013). This method is suitable to identify the watersheds and species that mostly contribute to the heterogeneity and compositional uniqueness of a biogeographic domain. For that, we assessed beta-diversity using the index proposed by Legendre and De Cáceres (2013). This index partitions the total beta-diversity (BDT) into the species contribution to beta-diversity (SCBD) and local (site) contribution to beta-diversity (LCBD); this measure of beta-diversity is estimated independently of local (α) and regional (γ) diversity. We used the *adespatial* package (Dray et al. 2021) to estimate the BDT, SCBD and LCBD indices using the *beta.div* function and the Hellinger transformation of the community matrix for each biogeographic domain. We excluded three watersheds from the analyses that had no native species.

SCBD values represent the relative contribution of species in the study area, interpreted here as the relative contribution of fish species to the total beta-diversity of each biogeographic domain. LCBD values indicate the uniqueness of the river watersheds (sampling units) in terms of the fish composition for each biogeographic domain. In a conservation perspective, species with high SCBD in the domain are those that mostly contribute to compositional variation amongst watersheds and should be prioritised in conservation efforts; and watersheds with high LCBD are those harbouring unique freshwater fish composition, being thus central to mitigate biotic homogenisation amongst watersheds.

Watershed contributions to beta-diversity

Watershed contributions to beta-diversity (LCBD) were mapped across the world according to species of all origin (native and non-native) to represent the "present-day" time-period and according to native species only to represent the "historical" time-period prior to non-native species introductions. In addition, the classification of native and non-native has a time limitation, as information prior to 1850 is difficult to secure. The change in LCBD was due to the introduction of non-native species ($\Delta LCBD = LCBD_{present} - LCBD_{historical}$). Positive ΔLCBD values indicate watersheds that have maintained or increased their contribution to beta-diversity in the present-day, whereas negative values indicate watersheds with decreasing contributions due to non-native species introductions. Next, we investigated the relationship between LCBD (and ΔLCBD) and the proportional richness of non-native species. Our expectation is that highly-invaded watersheds will exhibit LCBD decreases over time. We thus used a local polynomial regression fitting method (see Cleveland et al. 1992), which is suitable to investigate an overall trend that is not necessarily linear. We chose this method given our goal was to run an exploratory analysis without establishing a functional relationship. Therefore, trend strengths were described using only the R-squared fit, not p-values. We also investigated the overall trend between LCBD and present-day α diversity (number of fish species) for each watershed. A positive association would indicate that the watersheds most important for beta-diversity would be those with higher species richness. We

then compared LCBD between endorheic (river mouth is not at the ocean) and exorheic (river mouth is at the ocean) watersheds using a Welch two-sample t-test, given the lack of homoscedasticity (standard deviations were always different between groups). The complete database of LCBD values, total species richness and number of non-natives for all evaluated watersheds is available as Suppl. material 1. For all graphs and analyses, LCBD values were standardised (values scaled to zero mean and unit variance) within each domain to facilitate comparisons amongst domains that differed considerably in the number of watersheds and overall species richness.

Species contributions to beta-diversity

SCBD were calculated (and standardised as described for LCBD) for all species in each domain and related to relative species occupancy (%) calculated as the percentage of watersheds occupied by species, using local polynomial regression fitting method (Cleveland et al. 1992) to describe the overall trend, following the same justification as mentioned above for LCBD trends. We explored these relationships per domain separately (Suppl. material 1). Standardised SCBD were compared between species classified into two groups: 'Least concern' and those with some threat status (excluding the already extinct species, those not evaluated or those with data deficient) based on the IUCN threat categories of species (*sensu* <https://www.iucnredlist.org/en>) using Welch two-sample t-tests also given the lack of homoscedasticity. Finally, we described the five most important species (i.e. the highest SCBD) for each domain according to their origin, endemism, IUCN threat status and the following ecological characteristics (Froese and Pauly 2021):

i. Habitat: Euryhaline (EU) refers to species that can occupy environments of different salinities, but not necessarily for spawning; Freshwater (FRE) refers to species that occupy freshwater in the entire life cycle and may tolerate only mild estuarine conditions.
ii. Migration: Non-migratory (NM) species have sedentary behaviour and limited movements along the watershed; Potamodromous (PO) species migrate to spawn in freshwater ecosystems; Catadromous (CA) species live in freshwater and migrate to estuaries/oceans to spawn; Anadromous (ANA) species migrate up rivers from the oceans to spawn; Amphidromous (AM) species migrate from freshwater to saltwater or vice versa at some stage in their life cycle, but not necessarily to spawn.
iii. Vertical position in the water column: Demersal (DE) refers to species that live near or at the bottom of the aquatic environment; Bento-pelagic (BP) species live in the water column or at the bottom of the aquatic environment; Pelagic-neritic (PN) species occur in the water column and near littoral areas.

The complete database of SCBD values for all species, as well as their occupancy and origin (native or non-native) in the domains and the IUCN threat status (if available) is provided as Suppl. material 1. All analyses were performed in the R language (R Core Team 2024), graphs and polynomial regressions were generated using the *ggplot2* package (statistics were obtained using 'loess' function; Wickham 2016) and maps used the same watershed definitions, names and acronyms of Tedesco et al. (2017).

Results

Watersheds displayed marked variability in their contributions to fish beta-diversity, with these contributions changing in response to the inclusion of non-native species. We depicted historical LCBD in the left panels, where high values indicate basins with a unique freshwater composition and changes in LCBD due to non-native species in the right panels, with negative values indicating biotic homogenisation and positive values indicating differentiation (Fig. 1). In the Australian domain, the most contributing watersheds are located in Indonesia and Papua New Guinea, as well as in central and east Australia; whereas in west Australia, the watersheds demonstrated a decreased LCBD due to non-native species. In Ethiopia, the highest contributing watersheds are predominantly located in north and west Africa, as well as Middle East, with also small important watersheds in east Africa. Watersheds in south Africa were the ones that mostly changed due to the introduction of non-native species. Nearctic watersheds had LCBD values that varied substantially across space: the most important watersheds were located both in extreme south (mostly) and north of the domain; and those that mostly decreased LCBD due to non-native species are concentrated in the east and (mostly) west of USA and Canada. The most important watersheds in the Neotropic included both small watersheds near the Andes Mountains as well as the world's largest watershed, the Amazon. In this domain, the watersheds that mostly changed due to non-natives were generally also small near the Andes and one in northeast Brazil. Palearctic's most important watersheds were generally located in the southern tropical areas of the domain (except some in north and northeast Russia and small ones near the Mediterranean Region); and the most impacted watersheds include locations in the Middle East, several small watersheds in the Mediterranean Region and also in the UK. Finally, the Sino-Oriental domain had a relatively homogeneous geographic distribution of LCBD, but the most important were rarely in the north-eastern region of the domain. Watersheds with high changes were located in north-west China, Kirghizistan and Kazakhstan, as well as some small watersheds in Japan.

The relationship between the LCBD with and without non-native species is available for all domains in Fig. 2 and for each separate domain in Suppl. material 1. If the exclusion of non-native species does not change the watershed importance to beta-diversity, then the values would fall on the expected dashed line in figures. Patterns revealed those domains with watersheds harbouring more non-native species were Ethiopian, Nearctic, Palearctic and Sino-Oriental (Fig. 2). Accordingly, those were the domains in which LCBDs mostly changed. Watersheds with a high number of non-native species made were those that mostly varied from the expected mean (i.e. no change in LCBD), proportionally decreasing the LCBD with non-natives (i.e. values above the expected mean). Additionally, the watersheds with higher LCBD values were those with a higher proportion of non-native species for Ethiopian, Neotropical and Sino-Oriental domains (Fig. 2, Suppl. material 1). These three domains are those harbouring watersheds with the highest species richness. LCBD for Australian domain watersheds were the less variable (Fig. 2). See also Suppl. material 1 for graphs separated by domain.

By looking at the LCBD changes across domains, only the Australian domain did not have a clear negative relationship between changes in LCBD after removing non-native species and the proportion of non-natives, but the other domains do (Fig. 3).

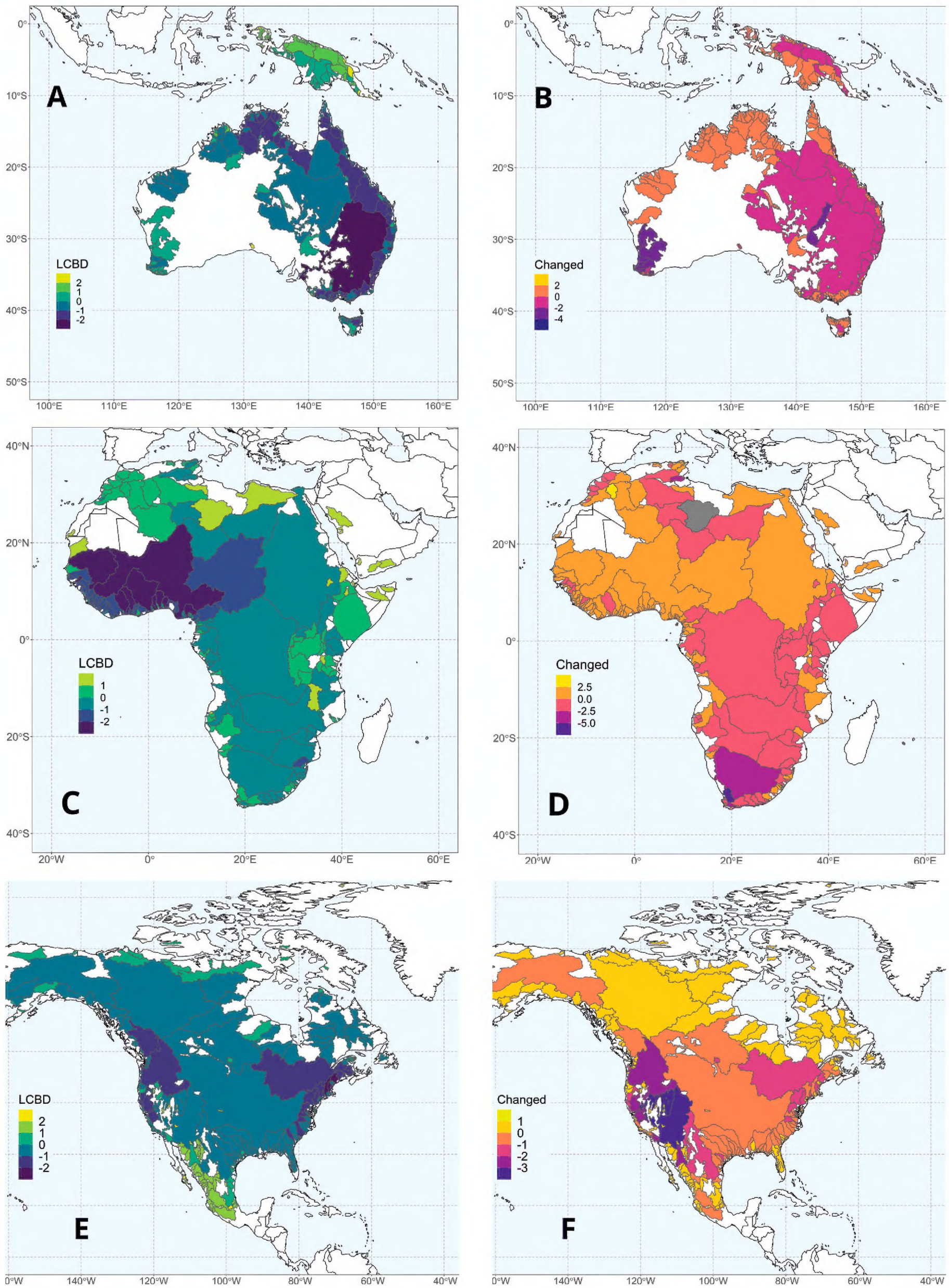

Figure 1. Maps for each biogeographical domain showing the local contribution to beta-diversity (LCBD) of watersheds with non-natives and the decrease in LCBD due to non-native species (Change = LCBD with non-natives – LCBD without non-natives) **A** LCBD – Australian **B** LCBD change – Australian **C** LCBD – Ethiopian **D** LCBD change – Ethiopian **E** LCBD – Nearctic **F** LCBD change – Nearctic **G** LCBD – Neotropical **H** LCBD change – Neotropical **I** LCBD – Palearctic **J** LCBD change – Palearctic **K** LCBD – Sino Oriental **L** LCBD change – Sino Oriental. Values were standardised per biogeographic domain for better comparisons amongst them.

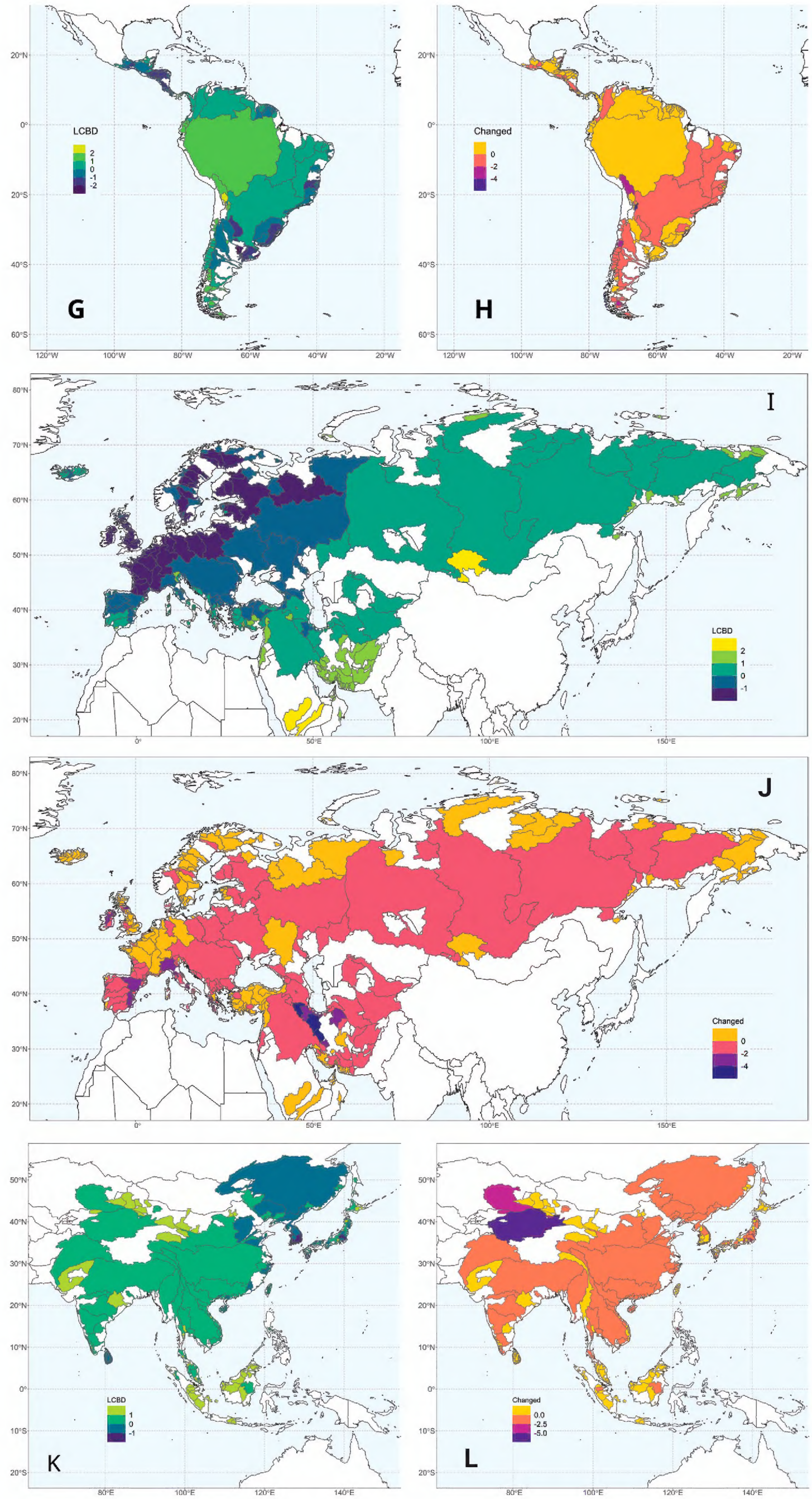

Figure 1. Continued.

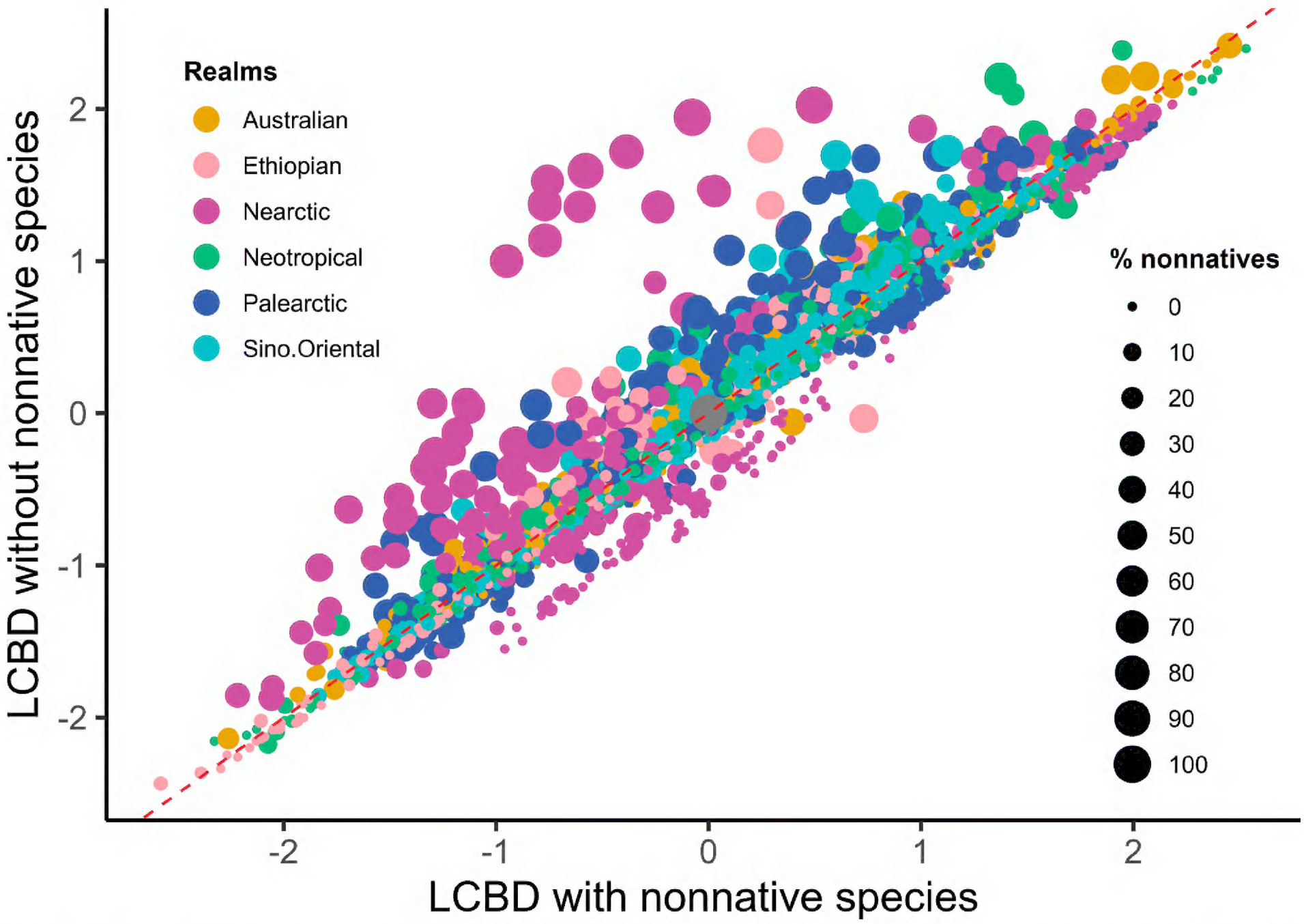

Figure 2. Relationship between standardised values of local contribution to beta-diversity (LCBD) with and without non-native species in each biogeographic domain. The size of the symbols indicates the proportion of non-native species and the colours indicate the domain. The red dashed line indicates the expected line of no change in LCBD. Graphs for each domain are available in Suppl. material 1.

Watershed species richness demonstrated weak associations with watershed contributions to beta-diversity (LCBD) (Fig. 4). The watersheds with the highest LCBD for each domain (those with unique conditions and species composition) rarely demonstrated high species richness. Even so, the watersheds with the highest species richness had LCBD values above average for Australian, Neotropical and Sino-Oriental domains (Fig. 4). The Suppl. material 1 summarises the features of the most important watershed in each biogeographical domain, including their nature (endorheic or exorheic) and overviews of species composition: IUCN status and endemism of species.

Although much less common worldwide (161 watersheds out of 2,760), endorheic watersheds had significantly higher LCBD (Fig. 4) in all domains (Welch two sample t-tests; $P < 0.001$), except Neotropical ($P = 0.775$) (Fig. 4). Detailing the features of the most important watersheds in each domain, it is clear that they included a unique species composition, with endemic and threatened species and most of them are endorheic (Suppl. material 1).

In general, SCDB values increased with occupancy (Fig. 5). SCBD was significantly higher for non-threatened species (Welch two sample t-tests; $P < 0.001$), except for Australian (Welch two sample t-tests; $P = 0.193$; see Fig. 5). Domain summaries are available in Suppl. material 1.

Native species always had the top five highest absolute SCBD values in all domains (Suppl. material 1), but non-natives had significantly higher mean SCBD

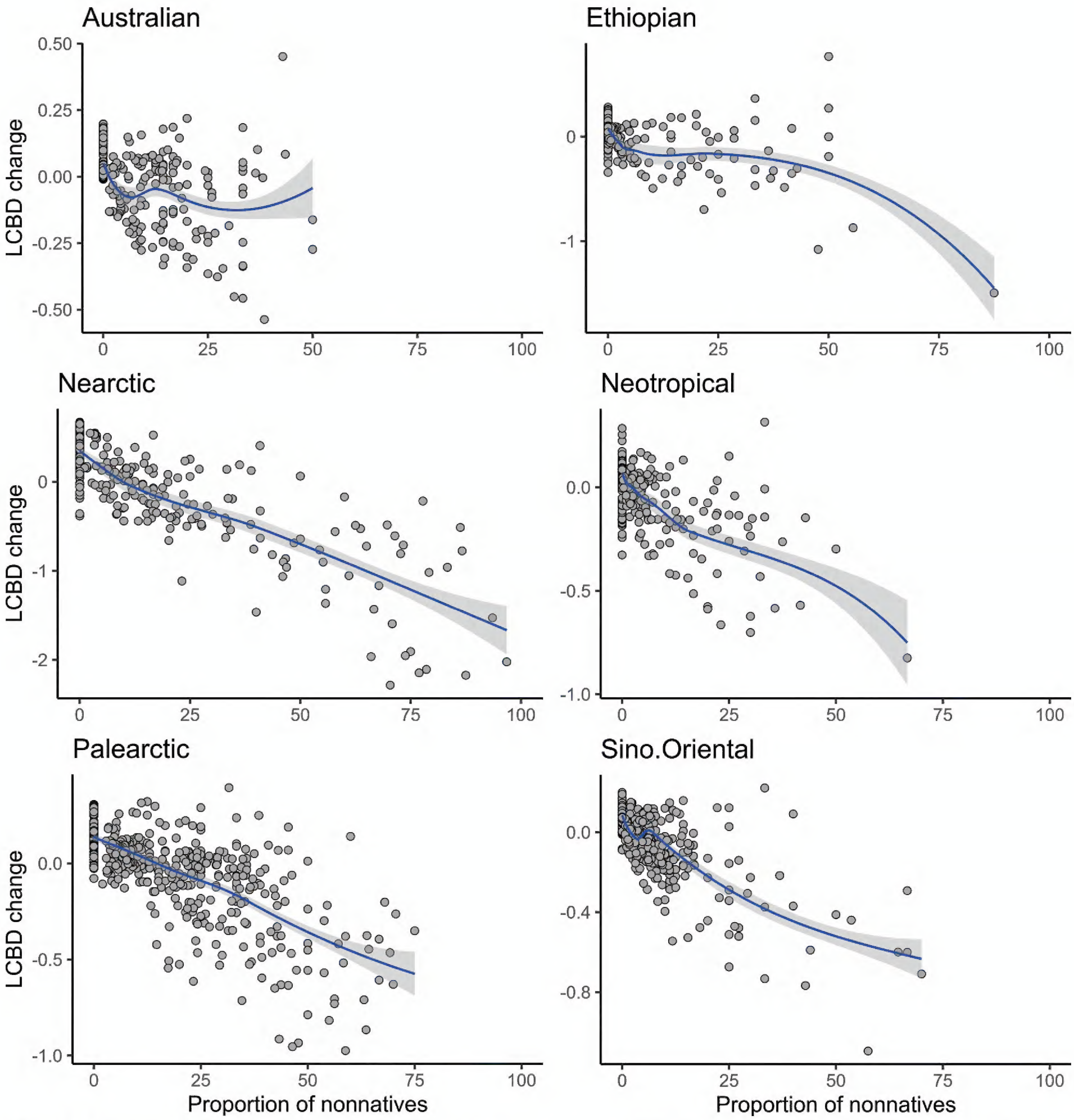

Figure 3. Changes in standardised values of local contribution to beta-diversity (LCBD change) considering values calculated with minus without non-native species against the proportion of non-native species (percentages) from each biogeographic domain. Curves indicate the best fit (grey areas are the standard errors) according to a local polynomial regression fitting method. R-squared were the following for each domain: Australian (28.4%); Ethiopian (40.0%); Nearctic (71.5%); Neotropical (47.6%); Palearctic (54.3%); Sino.Oriental (54.1%).

in Ethiopian and Neotropical domains (Welch two sample t-tests; $P = 0.008$ and $P = 0.04$, respectively, Fig. 5). The eastern mosquito fish *Gambusia holbrooki* (Girard, 1859) was the non-native species with the highest SCBD in three domains (8th in Australian, 6th in Ethiopian and 17th in Palearctic; native from Nearctic). The other non-native species with highest values in each domain were: the guppy fish *Poecilia reticulata* (Peters, 1859) (35th in Nearctic, native from Neotropical), the European trout *Salmo trutta* (Linnaeus, 1758) (7th in Neotropical, native from Palearctic) and the Mozambique tilapia *Oreochromis mossambicus* (Peters, 1852) (29th in Sino-Oriental, native from the Ethiopian).

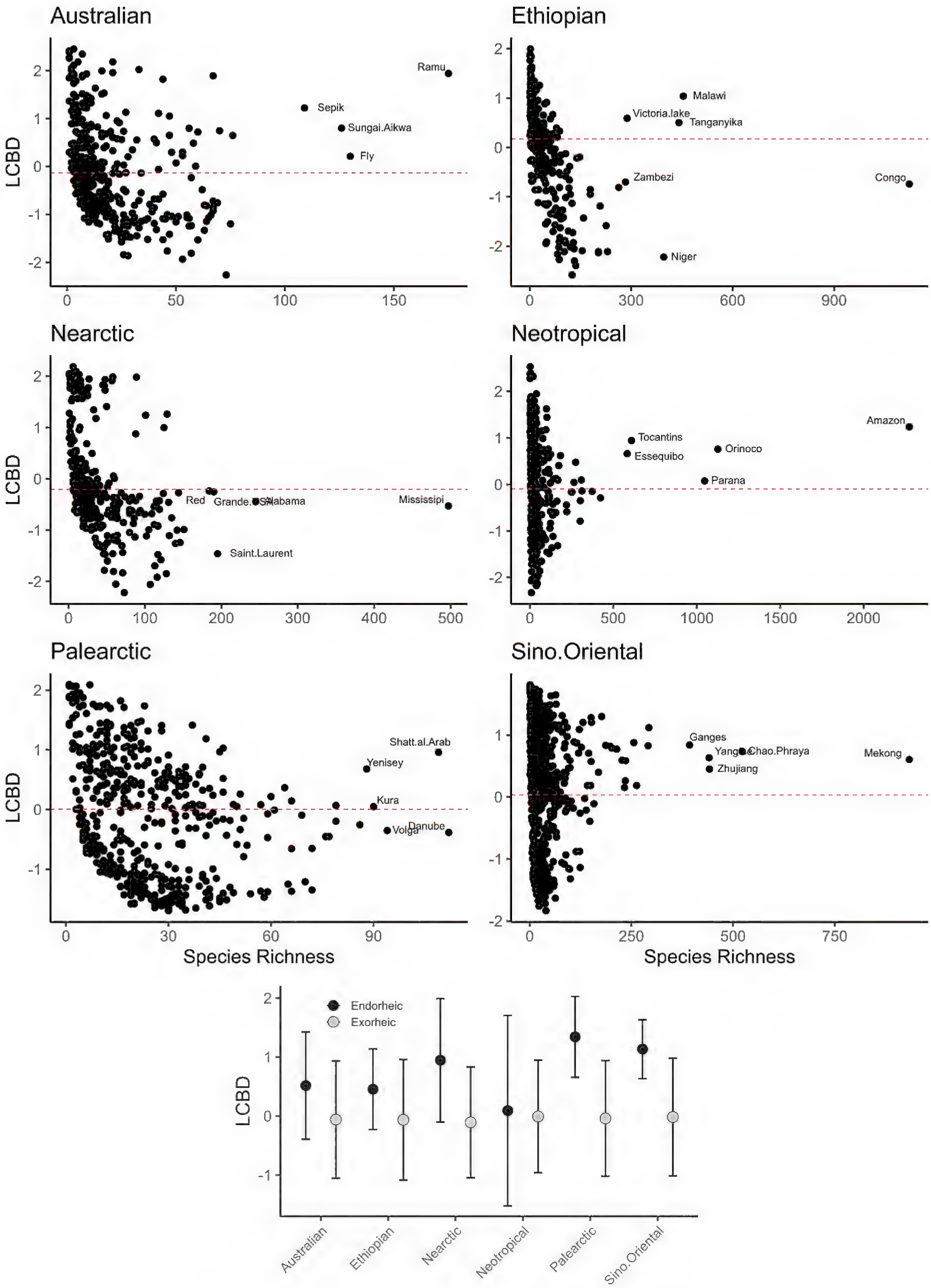

Figure 4. Relationship between standardised values of the local contribution of beta-diversity (LCBD) and species richness in the watersheds for each freshwater biogeographic domain (first six graphs). The horizontal red dashed line indicates the median value, so watersheds above it are the most important for species composition according to LCBD. Watersheds with the highest species richness were identified. Lower graph: means and standard deviations of the standardised LCBD for endorheic (black) and exorheic (grey) watersheds in the different biogeographic domains.

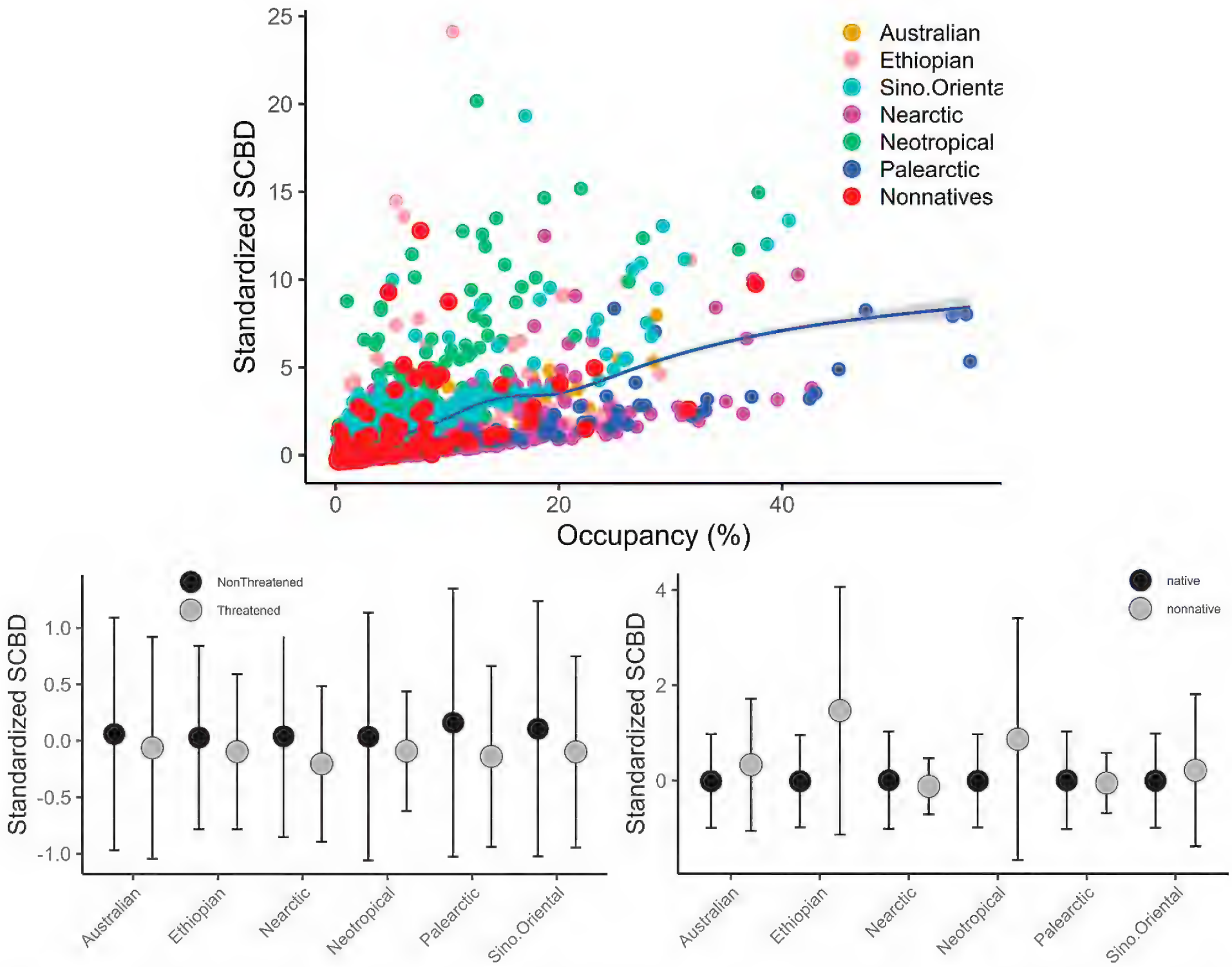

Figure 5. Upper middle: relationship between standardised values of species contribution to beta-diversity (SCBD) and relative species occupancy, estimated as the percentage of watersheds in which the species occur for biogeographic domains to which it belongs (R-squared to polynomial regressions = 51.6%). Values were standardised for each domain separately. Colours indicate standardised SCBD values for species in different biogeographic domains, red dots highlight the non-native species in biogeographic domains and blue lines indicate the best-fit curve (grey areas are the standard errors) using the local polynomial regression fitting method. Relationships for each biogeographic domain are available in the Suppl. material 1. Lower left: Means and standard deviations of standardised values of species contribution to beta-diversity (SCBD) between non-threatened (black) and threatened species (grey) *sensu* IUCN threat status in all biogeographic domains. Lower right: means and standard deviations of standardised values of species contribution to beta-diversity (SCBD) between native (black) and non-native species (grey) in all biogeographic domains.

Some patterns emerged amongst the top five species with the highest SCBD in each of these six domains: the majority of species were Euryaline, even though most species from the database live in freshwater or only tolerate estuaries (16 out of 30 species, 53.3%); a high prevalence of demersal or benthopelagic species (27 out of 30, 90.0%) and species with some migrating behaviour (18 out of 30, 60.0%); and five species (16.7%) having some reported IUCN vulnerability (three Endangered and two Near Threatened, see Suppl. material 1).

Discussion

Introductions by non-native species have fundamentally altered the global biogeography of freshwater fishes. This study demonstrates marked taxonomic and geographic differences in contributions to fish beta-diversity patterns of biogeographic

domains. Our results have important implications for national and international conservation initiatives that seek to preserve the uniqueness of the world's fish fauna.

We demonstrated a highly variable effect of non-native species on global-scale biogeographic patterns of freshwater fish. Despite this variability, in general, we found with increasing non-native species dominance comes greater reduction in LCBD and this effect occurred mainly in the domains with known human impacts (Leroy et al. 2023). This result is supported by continued evidence for fish faunal homogenisation being promoted by cosmopolitan non-native species replacing endemic native species over time (McKinney and Lockwood 1999). Indeed, evaluating the effect of non-natives at a global scale reveals the ability of invasions to reduce beta-diversity (Leprieur et al. 2008; Toussaint et al. 2016; Liu et al. 2017; Leroy et al. 2023). By highlighting the deterioration of beta-diversity by species invasions, our approach adds another piece to solve 'The Biodiversity Conservation Paradox' puzzle, in which Vellend (2017) argues that the number of species is not a good indicator for conservation priority without considering species origin and compositional variation, amongst other facets of biodiversity. We add our voices to the growing chorus that compositional uniqueness should be considered together with species richness in biodiversity assessments of conservation priorities.

It was clear that the Ethiopian, Nearctic, Palearctic and Sino Oriental are the domains in which the beta diversities of watersheds were mostly changed due to non-native species. Even so, we raised concerns in the Neotropical domain, given the watersheds with higher decreases in beta-diversity due to invasions were also those with higher importance for beta-diversity (see Fig. 2) in the most important domain for global fish biodiversity. The most important watersheds for such domains were those that have a great connection to coastal areas, in which marine freshwater-tolerant species (or vice versa) inhabit (see also Kong et al. 2017). This fact may even explain the watershed that increased LCBD due to the introduction of new species into the community from coastal and estuarine systems. The inclusion of freshwater non-native species may have influenced the taxonomic and even functional dissimilarity compared to other watersheds (Milardi et al. 2019). This rationale can also explain the fact that the Australian domain had watersheds that both increased (particularly those with low LCBD) and decreased (particularly those with high LCBD) beta-diversity due to non-native species, thus not resulting in a clear decrease pattern of LCBD with non-natives.

LCBD has been used as an important indicator of ecosystem uniqueness considering species composition (Bórquez et al. 2023). Our study reveals such important facets for global freshwater conservation: the watersheds that mostly contribute to beta-diversity in their domains are those with unique conditions that deserve conservation efforts. Although many context-dependent features may explain the uniqueness of watersheds, we could find some patterns: the most unique watersheds were not necessarily those with high species richness, they usually had high endemism, harbour species with IUCN threat status and, amongst them, endorheic watersheds deserve careful attention.

Endorheic watersheds are expected to be more unique and, at the same time, more susceptible to global changes due to their higher physical isolation and consequently high rates of species replacement and endemism (Levêque et al. 2008; Leprieur et al. 2011; Albert et al. 2020). Even though there were no significant differences in mean LCBD values for the Neotropical domain, the watershed with the highest LCBD values in this domain is a nice example: isolated and located

on the central plateau of the Andes (Bolivia-Argentina-Chile), 'Salina de Uyuni' is a unique place with low richness and high endemism of species that live under extreme salt and climatic conditions typical of the mountains. Although we did not find references to support the uniqueness of environmental conditions of this region, our results suggest that it should be better investigated and described in ecological studies. Indeed, only four genera of fish exist above 3,000 m in the Andean plateau, one of them recently described (Lacoste et al. 2020). Even so, mountain sites are currently threatened by the introduction of Salmonidae species (Vila et al. 2007; Aigo et al. 2008). Another extreme example can be observed in the endorheic watershed with the highest LCBD in the Nearctic: 'Bolson de Sandia' in Mexico. Five species from this watershed are now considered extinct or extinct in the wild according to the IUCN. Even without considering extinct species in our analyses, this watershed still had a high LCBD, harbouring a unique endemic species: the speckled flounder flatfish *Paralichthys woolmani* Jordan & Williams (1897). The second most important watershed in the Nearctic was also an endorheic watershed in Mexico: 'Bolson de Cuatro Cienegas', with all six fish species either endangered or critically endangered by IUCN. Finally, the top three watersheds with the highest LCBD in Palearctic were all endorheic and composed mainly of endemic species, including the IUCN-vulnerable *Salmo abanticus* Tortonese (1954).

The species-rich watersheds in biogeographic domains did not have the highest LCBD values, but some had above-average values. The high LCBD and species-rich watersheds are also endorheic in the Ethiopian domain: the ancestral lakes Victoria, Tanganyika and Malawi, all with a high level of cichlid endemism (Lévêque et al. 2008). These lakes have seen the introduction of translocated species that now hybridise and compete with native species, causing some populations to decline or disappear altogether (Cucherousset and Olden 2011). Other species-rich watersheds had also above-average LCBD values in other domains, such as the Amazon in Neotropical, Mekong in Sino Oriental, Ramu in Australian and Shatt al Arab in Palearctic. Such watersheds are also amongst the largest in their domains, with a well-documented high proportion of endemic species, very important for socio-economic activities and also recently impacted by species introductions (Fu et al. 2003; Jellyman et al. 2015; Albert et al. 2020).

The contribution of watersheds to freshwater beta-diversity is just one of many important metrics to consider with respect to prioritising conservation action. For the Ethiopian domain, the two watersheds with the highest LCBD were characterised by endangered and endemic species, but the watershed with the highest species richness had a below-average LCBD: the Congo River watershed. The Congo River watershed has a relatively low percentage of non-natives and is less impacted than other watersheds of similar richness (Su et al. 2021). Thus, the reasons for its low uniqueness should be related to multiple palaeo-connectivity and eco-evolutionary mechanisms (see also Carvajal-Leprieur et al. 2011). Undoubtedly, this river should always be a priority for freshwater fish conservation in Ethiopian domains, considering other reasons (biodiversity, ecological and economic relevance, large size etc.) apart from its compositional uniqueness.

Another watershed that is highly biologically diverse, but not unique considering LCBD is the Danube watershed in the Palearctic. This river has a long history of anthropogenic pressure and is a conservation priority due to pollution, land use, urbanisation, alteration of the hydrological regime and the introduction of species; which has resulted in the disappearance of many native species (Bănăduc et al. 2020). In the

Nearctic domain, the most iconic watershed has a similar situation: the Mississippi River watershed, considered the greatest refuge for freshwater fish and with a high degree of endemism in the domain (Dias et al. 2014), but with below-average LCBD probably due to the high number of non-natives (n = 66), the second-most invaded watershed after the Colorado River (see Suppl. material 1). Considering the high number of native species (n = 431), the proportion of non-natives in the Mississippi River may not be high, but the impacts of non-natives are usually disproportional and due to certain species (Britton 2022). Indeed, the invasion of one well-suited fish can disrupt most communities (e.g. Pelicice and Agostinho 2009) and impacts are even more disastrous in sites with high endemism (Daga et al. 2016).

More than focusing on watersheds, we also shed light on the most important species contributing to beta-diversity in each domain. As expected, SCBD generally increases with regional occupancy (Pozzobom et al. 2020), but, noticeably, the vast majority of species have lower than 50% occupancy. The most important species were almost exclusively native in origin and inhabited the bottom of the water column, mostly with euryhaline habitats and with some kind of migratory behaviour. The biology of such species explains their higher SCBD, given they may vary more than freshwater-only non-migratory fish amongst watersheds. Relatedly, saline tolerance is key in explaining fish composition and diversity in freshwater-marine transition zones (Whitfield 2015).

The loss of species with the largest contributions to beta-diversity is, thus, most likely to promote biotic homogenisation (Olden 2006). Such species could be the focus of regional conservation efforts to ensure longer-term persistence. We found little evidence that IUCN threatened species have higher SCBD values compared to unlisted species. This result is somewhat expected given such species may likely be rare, with low occupancy in their domain and, thus, contribute little to global beta-diversity. We reinforce that this result may never be interpreted as a reason not to focus on their conservation. Promoting their conservation may increase their occupancy and, consequently, their importance to beta-diversity. Even so, considering only the top five species with the highest SCBD values in each domain (n = 30), five of them already have an IUCN status of threat and we urge for their conservation. In the Nearctic, the two native trout species rainbow trout *Oncorhynchus mykiss* Walbaum (1792) and brook trout *Salvelinus fontinalis* Mitchill (1814) are amongst them, although they can be considered non-native species in some basins of North America and globally. Conservation of native trout in USA has become a matter of intense debate given their historical link to human culture (e.g. Willians et al. 2015); our study reinforces the relevance of this discussion. Related, the near-threatened Atlantic salmon *Salmo salar* (Linnaeus, 1758) is ranked as one of the most important species in the Palearctic to beta-diversity and is also one of the best studied and culturally valuable fish species in the Northern Hemisphere. Here, we only reinforce its importance to the Palearctic beta-diversity conservation. In the Australian domain, the IUCN near-threatened southern pygmy perch *Nannoperca australis* (Günther, 1861) also deserves careful attention. This species is one of the small non-commercial fish that receive less attention to conservation and is now threatened mainly due to barriers to riverine movement (Todd et al. 2017). Finally, the endangered Japanese eel *Anguilla japonica* (Temminck & Schlegel, 1846) is another well-known species given its cultural significance and is threatened by multiple factors, such as non-controlled fisheries, habitat degradation and climatic changes (Yadav et al. 2020).

Another interesting view on the most important species considering their SCBD is the diversity of orders. Amongst the 30 most important species for the different domains, there were 13 different orders, which reinforces the context-dependence of freshwater fish diversity and origin (see van der Sleen and Albert 2021). As expected given their high diversity worldwide, Cypriniformes had the highest number of species listed as the most important. However, Salmoniformes was the order with the second highest number of important species, although it is only the third most diverse order in the Palearctic and the fourth most diverse in the Nearctic, where there are more species with the highest SCBD (van der Sleen and Albert 2021).

Here, we interpret high SCBD values as a proxy of the relative importance of species to beta-diversity (*sensu* Legendre and De Cáceres 2013). For native species, it is an informative metric to conservation efforts. On the other hand, the SCBD values of non-natives indicate their importance in changing domain beta-diversity, thus can be interpreted as an important metric to management efforts. Considering the non-natives with the highest SCBD values in each domain, they coincide with the species listed as the most frequently introduced species worldwide (see Suppl. material 1, fig. 3 in Muñoz-Mas et al. 2023), reinforcing that introductions disrupt global patterns of beta-diversity.

Final remarks

Distributions of non-native species are closely linked with human activities (Bernery et al. 2022) and their impacts are related to the characteristics of the receiving ecosystem as well as their ability to colonise new environments (Hui et al. 2023). Our study reinforces this already well-known pattern of decreasing beta-diversity mainly in the most impacted Nearctic and Palearctic domains (Leroy et al. 2023). Here, we scaled down and advocated that watersheds in this now-called PAGNEA were the ones that mostly changed their relative importance given non-native species. However, we went further and provided a map of priority watersheds, their overall features and a rank of species that should be considered for conservation efforts that praise the uniqueness of aquatic ecosystems. We also provided insights into how watersheds and species are more or less important to the biogeographic domain beta-diversity. We hope that, together with other biodiversity facets, our study contributes to a better understanding of the biogeographical patterns of freshwater fish and effective conservation planning.

Acknowledgements

We are greatly thankful to Dr. Boris Leroy and Dr. Ali Serhan Tarkan for thoughtful reviews of a previous version of the manuscript, and also for helping us on providing new data and guidance for analyses.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

The first author acknowledges the support of the 'Coordenação de Aperfeiçoamento de Pessoal de Nível Superior' (CAPES), Funding Code 001. A.A.P. also acknowledges the 'Conselho Nacional para o Desenvolvimento Científico e Tecnológico' (CNP) for continuous financial sup-port (Process Number for current funding: 308648/2021-8).

Author contributions

Lorraine L. Cavalcante – conceptualization, data analysis, writing. Thiago V. T. Occhi – conceptualization, editing. Julian D. Olden – editing, writing. Andre A. Padial – conceptualization, data analysis, writing.

Author ORCIDs

Lorraine L. Cavalcante https://orcid.org/0000-0001-7893-0804
Thiago V. T. Occhi https://orcid.org/0000-0001-9746-4941
Julian D. Olden https://orcid.org/0000-0003-2143-1187
Andre A. Padial https://orcid.org/0000-0002-8766-5974

Data availability

The organised data used for all analyses are available as Supporting Information and were obtained from freely available global databases.

References

Aigo J, Cussac V, Peris S, Ortubay S, Gómez S, López H, Battini M (2008) Distribution of introduced and native fish in Patagonia (Argentina): Patterns and changes in fish assemblages. Reviews in Fish Biology and Fisheries 18(4): 387–408. https://doi.org/10.1007/s11160-007-9080-8

Albert JS, Tagliacollo VA, Dagosta F (2020) Diversification of Neotropical freshwater fishes. Annual Review of Ecology, Evolution, and Systematics 51(1): 27–53. https://doi.org/10.1146/annurev-ecolsys-011620-031032

Bănăduc D, Curtean-Bănăduc A, Pedrotti F, Cianfaglione K, Akeroyd JR (2020) Human Impact on Danube Watershed Biodiversity in the XXI Century. Springer Nature. https://doi.org/10.1007/978-3-030-37242-2

Bernery C, Bellard C, Courchamp F, Brosse S, Gozlan RE, Jarić I, Teletchea F, Leroy B (2022) Freshwater fish invasions: A comprehensive review. Annual Review of Ecology, Evolution, and Systematics 53(1): 427–456. https://doi.org/10.1146/annurev-ecolsys-032522-015551

Bórquez J, Sampertegui S, Wallberg BN, Coral-Santacruz D, Ruiz VH, Samollow PB, Gouin N, Bertin A (2023) Ecological uniqueness across multiple levels of biodiversity in a Chilean watershed. Aquatic Ecology 58: 139–158. https://doi.org/10.1007/s10452-023-10051-9

Britton JR (2022) Contemporary perspectives on the ecological impacts of invasive freshwater fishes. Journal of Fish Biology 103(4): 752–764. https://doi.org/10.1111/jfb.15240

Britton JR, Lynch AJ, Bardal H, Bradbeer SJ, Coetzee JA, Coughlan NE, Dalu T, Tricarico E, Gallardo B, Lintermans M, Lucy F, Liu C, Olden JD, Raghavan R, Pritchard EG (2023) Preventing and controlling nonnative species invasions to bend the curve of global freshwater biodiversity loss. Environmental Reviews 31(2): 310–326. https://doi.org/10.1139/er-2022-0103

Capinha C, Essl F, Porto M, Seebens H (2022) The worldwide networks of spread of recorded alien species. Proceedings of the National Academy of Sciences of the United States of America 120(1): e2201911120. https://doi.org/10.1073/pnas.2201911120

Carvajal-Quintero J, Villalobos F, Oberdorff T, Grenouillet G, Brosse S, Hugueny B, Tedesco PA (2019) Drainage network position and historical connectivity explain global patterns in fresh-

water fishes' range size. Proceedings of the National Academy of Sciences of the United States of America 116(27): 13434–13439. https://doi.org/10.1073/pnas.1902484116

Cleveland WS, Grosse E, Shyu WM (1992) Local regression models. In: Chambers JM, Hastie TJ (Eds) Statistical Models in S. Routledge, New York, 309-373. https://doi.org/10.1201/9780203738535-8

CABI (2021) Compendium Invasive Species. https://www.cabi.org/ISC

Cucherousset J, Olden JD (2011) Ecological impacts of nonnative freshwater fishes. Fisheries 36(5): 215–230. https://doi.org/10.1080/03632415.2011.574578

Daga VS, Debona T, Abilhoa V, Gubiani EA, Vitule JRS (2016) nonnative fish invasions of a Neotropical ecoregion with high endemism: A review of the Iguaçu River. Aquatic Invasions 11(2): 209–223. https://doi.org/10.3391/ai.2016.11.2.10

Darwin C (1859) On the Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life. John Murray, London. https://doi.org/10.5962/bhl.title.68064

Dias MS, Oberdorff T, Hugueny B, Leprieur F, Jézéquel C, Cornu JF, Tedesco PA (2014) Global imprint of historical connectivity on freshwater fish biodiversity. Ecology Letters 17(9): 1130–1140. https://doi.org/10.1111/ele.12319

Dray S, David B, Guillaume B, Daniel B, Sylvie C, Guillaume G, Thibaut J, Guillaume L, Pierre L, Naima M, Helene HW (2021) adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.3-14. https://CRAN.R-project.org/package=adespatial

Froese R, Pauly D (2021) FishBase. World Wide Web electronic publication. www.fishbase.org

Fu C, Wu J, Chen J, Wu Q, Lei G (2003) Freshwater fish biodiversity in the Yangtze River basin of China: Patterns. threats and conservation. Biodiversity and Conservation 12(8): 1649–1685. https://doi.org/10.1023/A:1023697714517

Hui C, Richardson DM, Landi P, Minoarivelo HO, Garnas J, Roy HE (2016) Defining invasiveness and invasibility in ecological networks. Biological Invasions 18(4): 971–983. https://doi.org/10.1007/s10530-016-1076-7

Hui C, Pyšek P, Richardson DM (2023) Disentangling the relationships among abundance, invasiveness and invasibility in trait space. npj. Npj Biodiversity 2(1): 13. https://doi.org/10.1038/s44185-023-00019-1

Jellyman DJ, Gehrke PC, Harris JH (2015) Freshwater fisheries of Australasia. In: Craig JF (Ed.) Freshwater Fisheries Ecology. Wiley, New Jersey, 404–418. https://doi.org/10.1002/9781118394380.ch32

Kong H, Chevalier M, Laffaille P, Lek S (2017) Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system. PLoS ONE 12(3): e0174582. https://doi.org/10.1371/journal.pone.0174582

Kunming–Montreal Global Biodiversity Framework (2022) Kunming-Montreal Global Biodiversity Framework. https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf

Lacoste FF, Bize JA, Fernández L (2020) First record sheds light on the distribution of the cyprinodontiform genus *Jenynsia* (Günther. 1866) in the High Andean Plateau. Journal of Fish Biology 97(5): 1590–1594. https://doi.org/10.1111/jfb.14525

Legendre P, De Cáceres M (2013) Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecology Letters 16(8): 951–963. https://doi.org/10.1111/ele.12141

Leprieur F, Beauchard O, Blanchet S, Oberdorff T, Brosse S (2008) Fish invasions in the world's river systems: When natural processes are blurred by human activities. PLoS Biology 6(2): e28. https://doi.org/10.1371/journal.pbio.0060028

Leprieur F, Olden JD, Lek S, Brosse S (2009) Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. Journal of Biogeography 36(10): 1899–1912. https://doi.org/10.1111/j.1365-2699.2009.02107.x

Leprieur F, Tedesco PA, Hugueny B, Beauchard O, Dürr HH, Brosse S, Oberdorff T (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecology Letters 14(4): 325–334. https://doi.org/10.1111/j.1461-0248.2011.01589.x

Leroy B, Dias MS, Giraud E, Hugueny B, Jézéquel C, Leprieur F, Oberdorff T, Tedesco PA (2019) Global biogeographical regions of freshwater fish species. Journal of Biogeography 46(11): 2407–2419. https://doi.org/10.1111/jbi.13674

Leroy B, Bellard C, Dias MS, Hugueny B, Jézéque C, Leprieur F, Oberdorff T, Robuchon M, Tedesco PA (2023) Major shifts in biogeographic regions of freshwater fishes as evidence of the Anthropocene epoch. Science Advances 9(46): eadi5502. https://doi.org/10.1126/sciadv.adi5502

Lévêque C, Oberdorff T, Paugy D, Stiassny MLJ, Tedesco PA (2008) Global diversity of fish (Pisces) in freshwater. In: Balian EV, Lévêque C, Segers H, Martens K (Eds) Freshwater Animal Diversity Assessment. Developments in Hydrobiology 198. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-8259-7_53

Liu C, He D, Chen Y, Olden JD (2017) Species invasions threaten the antiquity of China's freshwater fish fauna. Diversity & Distributions 23(5): 556–566. https://doi.org/10.1111/ddi.12541

Marr SM, Olden JD, Leprieur F, Arismendi I, Ćaleta M, Morgan DL, Nocita A, Šanda R, Tarkan AS, García-Berthou E (2013) A global assessment of freshwater fish introductions in mediterranean-climate regions. Hydrobiologia 719(1): 317–329. https://doi.org/10.1007/s10750-013-1486-9

McKinney ML, Lockwood JL (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14(11): 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Milardi M, Gavioli A, Soininen J, Castaldelli G (2019) Exotic species invasions undermine regional functional diversity of freshwater fish. Scientific Reports 9(1): 17921. https://doi.org/10.1038/s41598-019-54210-1

Muñoz-Mas R, Essl F, van Kleunen M, Seebens H, Dawson W, Casal CMV, García-Berthou E (2023) Two centuries of spatial and temporal dynamics of freshwater fish introductions. Global Ecology and Biogeography 32(9): 1632–1644. https://doi.org/10.1111/geb.13714

Olden JD (2006) Biotic homogenization: A new research agenda for conservation biogeography. Journal of Biogeography 33(12): 2027–2039. https://doi.org/10.1111/j.1365-2699.2006.01572.x

Olden JD, Kennard MJ, Pusey BJ (2008) Species invasions and the changing biogeography of Australian freshwater fishes. Global Ecology and Biogeography 17(1): 25–37. https://doi.org/10.1111/j.1466-8238.2007.00340.x

Olden JD, Kennard MK, Leprieur F, Tedesco PA, Winemiller KO, García-Berthou E (2010) Conservation biogeography of freshwater fishes: Past progress and future directions. Diversity & Distributions 16(3): 496–513. https://doi.org/10.1111/j.1472-4642.2010.00655.x

Olden JD, Comte L, Giam X (2018) The Homogocene: A research prospectus for the study of biotic homogenisation. NeoBiota 37: 23–36. https://doi.org/10.3897/neobiota.37.22552

Padial AA, Vitule JRS, Olden JD (2020) Preface: Aquatic Homogenocene-understanding the era of biological re-shuffling in aquatic ecosystems. Hydrobiologia 847(18): 3705–3709. https://doi.org/10.1007/s10750-020-04413-9

Pagad S, Genovesi P, Carnevali L, Scalera R, Clout M (2015) IUCN SSC Invasive Species Specialist Group: Invasive alien species information management supporting practitioners, policy makers and decision takers. Management of Biological Invasions 6(2): 127–135. https://doi.org/10.3391/mbi.2015.6.2.03

Pelicie FM, Agostinho AA (2009) Fish fauna destruction after the introduction of nonnative predator (Cichla kelberi) in a Neotropical reservoir. Biological Invasions 11(8): 1789–1801. https://doi.org/10.1007/s10530-008-9358-3

Pelicice FM, Agostinho AA, Azevedo-Santos VM, Bessa E, Casatti L, Garrone-Neto D, Gomes LC, Pavanelli CS, Petry AC, Pompeu PS, Reis RE, Roque FO, Sabino J, Sousa LM, Vilella FS, Zuanon J (2023) Ecosystem services generated by Neotropical freshwater fishes. Hydrobiologia 850: 2903–2926. https://doi.org/10.1007/s10750-022-04986-7

Pozzobom UM, Haino J, Brito MTS, Landeiro VL (2020) Untangling the determinants of macrophyte beta diversity in tropical floodplain lakes: Insights from ecological uniqueness and species contributions. Aquatic Sciences 82(3): 56. https://doi.org/10.1007/s00027-020-00730-2

Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak N, Meyerson L, Pauchard A, Pergl J, Roy HE, Seebens H, van Hleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. Biological Reviews of the Cambridge Philosophical Society 95(6): 1511–1534. https://doi.org/10.1111/brv.12627

R Core Team (2024) R: A language and environment for statistical computing. RFoundation for Statistical Computing. Vienna, Austria. https://www.R-project.org/

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): 14435. https://doi.org/10.1038/ncomms14435

Skóra F, Abilhoa V, Padial AA, Vitule JRS (2015) Darwin's hypotheses to explain colonization trends: Evidence from a quasi-natural experiment and a new conceptual model. Diversity & Distributions 21(5): 583–594. https://doi.org/10.1111/ddi.12308

Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? Trends in Ecology & Evolution 31(1): 67–80. https://doi.org/10.1016/j.tree.2015.11.005

Su G, Villéger S, Brosse S (2019) Morphological diversity of freshwater fishes differs between realms. but morphologically extreme species are widespread. Global Ecology and Biogeography 28(2): 211–221. https://doi.org/10.1111/geb.12843

Su G, Logez M, Xu J, Tao S, Villéger S, Brosse S (2021) Human impacts on global freshwater fish biodiversity. Science 371(6531): 835–838. https://doi.org/10.1126/science.abd3369

Tedesco PA, Leprieur F, Hugueny B, Brosse S, Dürr HH, Beauchard O, Busson F, Oberdorff T (2012) Patterns and processes of global riverine fish endemism. Global Ecology and Biogeography 21(10): 977–987. https://doi.org/10.1111/j.1466-8238.2011.00749.x

Tedesco P, Beauchard O, Bigorne R, Blanchet S, Buisson L, Conti L, Cornu JF, Dias MS, Grenouillet G, Hugueny B, Jézéquel C, Leprieur F, Brosse S, Oberdorff T (2017) A global database on freshwater fish species occurrence in drainage basins. Scientific Data 4(1): 1–6. https://doi.org/10.1038/sdata.2017.141

Tickner D, Opperman JJ, Abell R, Acreman M, Arthington AH, Bunn SE, Cooke SJ, Dalton J, Darwall W, Edwards G, Harrison I, Hughes K, Jones T, Leclère D, Lynch AJ, Leonard P, Mc ME, Clain D, Muruven JD, Olden SJ, Ormerod J, Robinson RE, Tharme M, Thieme K, Tockner M, Wright L, Young L (2020) Bending the curve of global freshwater biodiversity loss – an emergency recovery plan. Bioscience 70(4): 330–342. https://doi.org/10.1093/biosci/biaa002

Todd CR, Koehn JD, Pearce L, Dodd L, Humphries P, Morrogiello JR (2017) Forgotten fishes: What is the future for small threatened freshwater fish? Population risk assessment for southern pygmy perch, *Nannoperca australis*. Aquatic Conservation 27(6): 1290–1300. https://doi.org/10.1002/aqc.2808

Toussaint A, Beauchard O, Oberdorff T, Brosse S, Villéger S (2016) Worldwide freshwater fish homogenization is driven by a few widespread nonnative species. Biological Invasions 18(5): 1295–1304. https://doi.org/10.1007/s10530-016-1067-8

van der Sleen P, Albert JS (2021) Patterns of freshwater wetland fish species diversity. In: Tockner K, Mehner T, Wittmann F, Junk WJ (Eds) Encyclopedia of Inland Waters, Vol. 3, 2nd edn. Elsevier, Amsterdam, 243–255. https://doi.org/10.1016/B978-0-12-819166-8.00056-6

Vellend M (2017) The Biodiversity Conservation Paradox. American Scientist 105(2): 94–101. https://doi.org/10.1511/2017.105.2.94

Vila I, Pardo R, Scott S (2007) Freshwater fishes of the Altiplano. Aquatic Ecosystem Health & Management 10(2): 201–211. https://doi.org/10.1080/14634980701351395

Whitfield AK (2015) Why are there so few freshwater fish species in most estuaries? Journal of Fish Biology 86(4): 1227–1250. https://doi.org/10.1111/jfb.12641

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21(2–3): 213–251. https://doi.org/10.2307/1218190

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. Springer, New York, 189–201. https://doi.org/10.1007/978-3-319-24277-4_9

Willians JE, Haak AL, Fesenmyer K, Dauwalter DC, Neville HM, Barney M, Mayfield M (2015) State of the Trout. Executive summary, Trout Unlimited. https://www.tu.org/science/science-engagement/science-synthesis/state-of-the-trout/

Xia Z, Heino J, Yu F, He Y, Liu F, Wang J (2022) Spatial patterns of site and species contributions to β diversity in riverine fish assemblages. Ecological Indicators 145: 109728. https://doi.org/10.1016/j.ecolind.2022.109728

Xu M, Li S, Liu C, Tedesco PA, Dick JTA, Fang M, Wei H, Yu F, Shu L, Wang X, Gu D, Mu X (2024) Global freshwater fish invasion linked to the presence of closely related species. Nature Communications 15(1): 1411. https://doi.org/10.1038/s41467-024-45736-8

Yadav VK, Pandey S, Kaushlik P (2020) A brief perspective on Japanese eel (*Anguilla japonica* Temminck & Schlegel,1846) an indispensable part of Japanese culture. Indian Journal of Geo-Marine Sciences 49: 933–939.

Supplementary material 1

Supporting information

Authors: Lorraine L. Cavalcante, Thiago V. T. Occhi, Julian D. Olden, Andre A. Padial

Data type: zip

Explanation note: 1) LCBD-Cavalcante_et_al-Available.csv 2) SCBD-Cavalcante_et_al-Available.csv 3) Occurrence_Data.csv 4) Relationship between standardised values of local contribution to beta-diversity (LCBD) with and without non-native species in each biogeographic domain 5) Relationship between species contribution to beta-diversity (SCBD) and relative species occupancy, estimated as the percentage of watersheds in which the species occur for the different biogeographic domains 6) Means and standard deviations of standardised values of species contribution to beta-diversity (SCBD) for all IUCN threat categories for each domain separately and for all domains together 7) Watersheds (according to Tedesco et al. 2017) with the highest beta-diversity (LCBD, all with similar values after five decimal num-bers) in each biogeographic domain and their species composition.

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.97.126607.suppl1